Studies in Cyperaceae in southern Africa 32: *Eleocharis* subgenus *Limnochloa* section *Limnochloa*

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A taxonomic treatment of *Eleocharis* R. Br. subgen. *Limnochloa* (P. Beauv. ex Lestib.) C.B. Clarke sect. *Limnochloa* (P. Beauv. ex Lestib.) Bentham [=ser. Mutatae Svenson] is given for southern Africa. A key is provided for the identification of five species, *E. dulcis* (Burm.f.) Hensch., *E. acutangula* (Roxb.) Schult., *E. mutata* (L.) Roem. & Schult., *E variegata* (Poir.) Presl and *E. decoriglumis* Berhaut. Several of these taxa display a highly variable floral morphology that has been documented in the literature without adequate explanation having been given for its occurrence. The speculation is made that within a water body in which *Eleocharis* species are sympatric, introgression may be of long standing, the hybrid progeny usually co-existing with the putative parents so that a wide range of variability may be represented. *E. mutata* and *E. variegata* are interpreted as of hybrid origin. *E. mutata* and *E. decoriglumis* are recent new records for southern Africa.

Key words: *Eleocharis* subgen. *Limnochloa*, fresh water habitats, introgression, southern Africa, taxonomy, variability.

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Introduction

Eleocharis R. Br., with worldwide distribution, is a well demarcated, highly specialised genus (Kukkonen 1990: 109) usually placed within the tribe Scirpeae Kunth ex Dumort. (Tucker 1987: 384; Kukkonen 1990: 109; Bruhl 1995: 203). However, Goetghebeur (1986: 375) segregated it, with its two close relatives *Egleria* L.T. Eiten and *Websteria* S.H. Wright, as a new tribe *Eleocharideae* Goetghebeur.

A number of unusual features exhibited by the genus are already well known. These include spikelet conformation (Svenson 1929: 127–129; Kukkonen 1990: 109, 111); increase in number of adaxial perianth bristles by branching (Svenson 1929: 126; Blaser 1941: 549); often a low level of fruit set (Shah 1964: 43); a capacity in some species for vegetative growth from the inflorescence (La Rue 1936: 107) and polycentric chromosomes that are capable of fragmentation and reunion (agmatoploidy) (Löve *et al.* 1957, who quote Battaglia 1954 and Håkansson 1954). Agmatoploidy is a phenomenon that is not yet fully understood in relation to plant speciation (Grant 1971: 270). Polyploidy is also known for the genus (Tucker 1987: 388), as is hybridisation in the wild between species that would normally be regarded as too distantly related to permit the effective survival of progeny (Catling 1994: 837).

In southern Africa, although well represented in most wetland systems where fresh water predominates, the genus is poorly known. Habitat requirements and reproductive capacities have never been investigated. With attempts now being made to re-establish vleis and to colonise man-made water enclosures, the genus merits study. This paper reviews taxonomically, members of *Eleocharis* subgen. *Limnochloa* section *Limnochloa* known for southern Africa. These rhizomatous perennials, growing usually sympatrically, often in water bodies isolated from other comparable habitats, possess the attributes for introgression. From study of their morphology, we speculate that hybridisation has played, and still does play, an important role in relation to their variability and, no doubt, eventual speciation.

Formal taxonomy

Subgenus and Section

Eleocharis R. Br. Subgen. ***Limnochloa*** (P. Beauv. ex Lestib.) C.B. Clarke. In: Flora of Tropical Africa, ed. W.T. Thiselton-Dyer, 8: 405 (1901/02). Genus *Limnochloa* P. Beauv. ex Lestib.: 41 (1819) (no species named); Nees: 114 (1834); Nees: 294 (1835) (Nees' treatment includes the type species). Type: *E. mutata* (L.) Roem. & Schult. [selected by Koyama: 85 (1961)]

Section ***Limnochloa*** (P. Beauv. ex Lestib.) Benth. In: Bentham & Hooker, Genera Plantarum 3: 1047 (1883); Kukkonen: 112 (1990). Sect. Mutatae (Svens.) Egor & Khoi: 60 (1890); Series Mutatae Svens.: 127 (1929) Type: as for the Subgenus.

Diagnostic Features

Members of this subgenus and section are the tallest examples of *Eleocharis* known. Plants require permanent fresh water two to three metres in depth with a more or less stable level, whereas members of the other subgenera occur where fluctuating water depths may leave plants periodically exposed (Tucker 1987: 385).

The southern African representatives; except *E. decoriglumis* which is described as annual, but confirmation is needed; are robust, stoloniferous perennials with leaves reduced to delicate, membranous, eligulate sheaths that envelop only a short, basal portion of a culm. The spikelets are scarcely, or not, wider than the culm apices; the florets function reproductively only after emergence from water. Glumes are hard, persistent and usually indistinctly keeled.

There is no karyological information for southern African plants. From other continents chromosome numbers are high, for example Australia where 2n = nos. between 100 and 188 (Briggs 1970).

In America (Svenson 1929: 129–163); in Malaysia (Kern 1974; 525–531) and in West Tropical Africa (Hooper 1972: 314), representatives have proved problematical taxonomically. Menapace (1991) undertook a micromorphological analysis of *Eleocharis* achenes for systematic potential. His findings for Séries Mutatae were not conclusive.

Key to species

1a. Culms terete, hollow, septate with numerous transverse diaphragms mostly visible externally. Glumes oblong-elliptic, faintly longitudinally nerved distally (viewed abaxially × 20), not keeled. Style base long, pyramidal. Achene mouth an upstanding rim just more than half maximum achene width, from which style base arises directly; achene surface smooth. Perianth usually of 7, white, robust, retrorsely barbed bristles well surpassing achene in length (Figures 1, 4A and 6) ..... ***1. E. dulcis***

1b. Culms always lacking externally visible transverse septa; other features differing in some way(s) from contrast **2**

2a. Style branches consistently 2. Stamens 1 or 2 per floret. Glumes olive green, marked distally with a dark, purplish-brown, almost black band up to 0.5 mm deep, surmounted by a very narrow membranous edge. Plants lacking stolons, possibly annual ... ***5. E. decoriglumis***

2b. Style branches 3, or 2 and 3 within an inflorescence. Glumes, if marked distally with a dark band, then this brown or reddish-purple (not almost black) and surmounted by a clearly defined, sometimes very wide, zone of pallid membrane that wears away with age **3**

3a. Achene narrowed distally to about *one third or less of maximum achene width* to form a short neck with expanded rim; style base completely rounded over this (Figure 2A), or with margin uplifted to form a curled edge (Figure 2B) or fitting into it so that the achene neck is clearly defined (Figure 2C). All three possibilities may be represented within a single inflorescence (Figures 2, 4B, 4C and 7) ..... ***2. E. acutangula***

3b. Achene apex exceeding half maximum achene width, forming a rim to which the style base is attached. Style base *never* extending over the rim to cover it (Figures 3 and 5) **4**

4a. Glume oblong with a wide membranous apex up to one-third glume length that becomes ragged before wearing away with age; glume tissue marked by numerous dark dots (especially on inner, adaxial surface). Achene mouth hardly narrower than maximum achene width; achene surface lustrous, spongy, faintly or more strongly marked by longitudinal rows of cells, each cell transversely oblong or almost square. Culms variable, terete to 3–4 angled, often irregular and twisted, occasionally flattened (Figures 8 and 9A). ..... ***4. E. variegata***

4b. Glume about as long as wide (approx. 4.0 × 3.5 mm) with narrow, pallid membranous edge demarcated from remainder of glume by a brown line that fades with age; central tissue lacking clear venation except for median ridge that terminates before glume apex; dark dots usually lacking (Figure 4D). Achene mouth about three-quarters of maximum achene width, an erect, sometimes incurved ring meeting style base; achene surface not lustrous, spongy, strongly marked by many longitudinal rows of small cells only slightly elongated transversely (Figure 5). Culms markedly 3-angled throughout; sometimes twisted (Figures 3, 4D and 5) ..... ***3. E. mutata***

Enumeration of species

1. ***Eleocharis dulcis*** *(Burm.f.) Hensch.* Vita G.E. Rumphii: 186 (1833); Svenson: 158 (1929); Kern: 529 (1974); Hooper: 313 (1972); Haines & Lye: 66 (1983). Type: East Indies, based on *Cyperus dulcis* Rump. Herb. Amb. 6: 7 (1750). *Andropogon dulce* Burm. f.: 219 (1768), *n.v.*

Scirpus plantaginoides Rottb.: 45 (1773). Type from India. *n.v.* *S. plantagineus* Retz.: 14 (1788). *Eleocharis plantaginea* (Retz.) Roem. & Schult.: 150 (1817); C.B. Clarke: 405 (1901/02). Type: India, *Koenig, n.v.*

Figure 1 *Eleocharis dulcis*. **A.** Achene with perianth and style base. **B.** External topography of pericarp. **C.** Exocarp cells revealed by removal of outer periclinal walls. A,B. *Michelmore 42* (PRE). C. *Ellis 2734* (PRE). Scale bars. A. 500 µm, B. 25 µm, C. 100 µm.

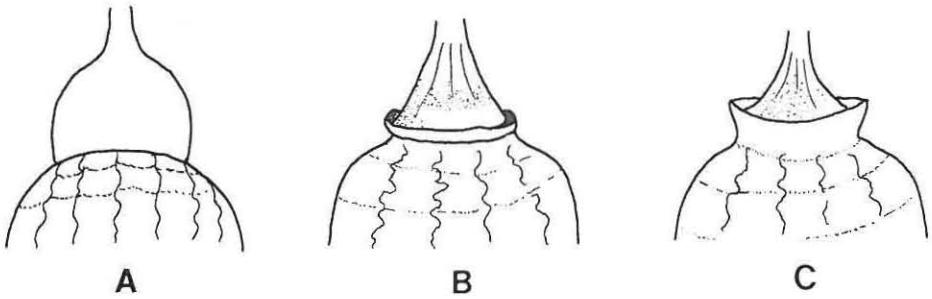

Figure 2 *Eleocharis acutangula.* Variation in style base. **A.** Turgid base rounded over achene neck. **B.** Margin of base uplifted on drying. **C.** Undeveloped base fitting into achene neck.

Perennial, tufted, shoot bases frequently dark red. *Rhizome* vertical, woody, up to 70 × 12 mm; stolons elongate, up to 350 mm before rooting and terminating in an erect shoot, nodose, internodes up to 75 × 6 mm, dark red or brown, nude except for scale leaves 5–8 mm long at nodes, soon wearing away; tubers lacking. *Culms* immersed in life except for distal apices, erect, terete, smooth, grey-green, septate, easily compressible, hollow except for numerous transverse diaphragms 3–5 mm apart (only visible externally at ± 700 mm intervals), variable in size, 0.5–2.7 m × 1–8 mm (see also under morphological notes). *Leaves* reduced to 2 entire, dark red to brown, delicate sheaths enveloping culm base (that is, prophyll and following sheath), uppermost sheath when intact up to 330 mm long, mouth oblique; ligule lacking. *Inflorescence* a terminal, lanceolate spikelet, cylindric in x-section, 65–70 × 4–5 mm. *Bract* 1, glume-like, hard, appearing veinless. *Glumes* regularly spirally imbricate, narrowly oblong-elliptic, 7–8 × 4–4.5 mm, not keeled, slightly folded basally, coriaceous, grey green passing into dark brown submarginal zone that fades with age, distal central zone, finely and faintly nerved (visible ×20), margin a narrow membrane soon wearing away. *Perianth* (perigonium) usually of 7 robust bristles (5 abaxial, 2 adaxial by branching), united basally forming persistent collar shed with achene, strongly retrorsely spinulose, surpassing achene. *Stamens* 3, falling early, anthers ± 2.5 mm long, apiculate crest 0.3 mm. *Style* flattened, base long pyramidal, persistent, fitting rim on achene apex; branches 3. *Achene* biconvex, urn-shaped to elliptic in outline, narrowed subterminally into a rim just wider than ½ achene width, 2.0–2.75 × 1.75–1.95 mm excluding style base, creamy white to pale brown; surface smooth, faintly cellular at ×600, cells longitudinally oblong (clearly visible when outer surface removed) (Figures 1, 4A and 6).

Morphological notes, including variability.

Stolons

Plants growing in deep water at Lake Nhlabane (voucher specimens: *C.J. Ward & A. Rajh 11459, 11464, 11597, 11599, 11718*) were characterised each by a vertical woody rhizome that produced radiating stolons along the underwater soil surface or close above it. These, after lateral extension up to 350 mm, terminated by vertical upgrowth. In all examples examined, every node along stolon length lacked adventitious roots and an axillary shoot bud. In this *E. dulcis* differed from the other species of section *Limnochloa* treated here. The dimensions of the vertical rhizome, in this and in other species dealt with, must indicate a considerable period of survival of the individual organism.

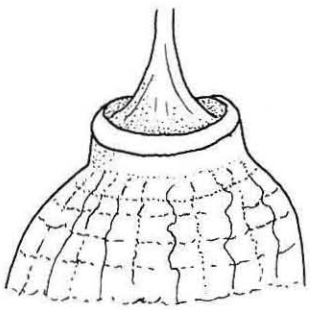

Figure 3 *Eleocharis mutata.* Style base fitting within achene rim (slightly shrunken by drying).

Culms

Parameters from living and freshly pressed specimens from Lake Nhlabane, (vouchers: as given under stolons) were as follows: in permanent water with a more or less stable depth of 2–3 m, plants were exceedingly robust with culms 2.5–2.7 m × 6–8 mm; in water about 0.45 m deep, culms were 0.5–0.6 m × 2–5 mm. The culms that terminated stolons were always less robust than those produced from a vertical rhizome. The most robust plants, all sterile at time of collection, borne from the same rhizomes as produced the robust culms, totally submerged, sterile, septate, bright green, translucent, filiform culms approximately 1 m × 1 mm. These were firmly attached and were neither seedlings, nor epiphytic growths. They were not observed on plants from shallower water. This peculiarity of a range in culm width of 1–8 mm from one rhizome at the same time seems phenomenal, but study of exsiccatae, particularly from the Okavango swamps [*P.A. Smith 455; 2663* (PRE)], and reference to literature has revealed that such variability is not exceptional for *E. dulcis*. Kern (1974: 530) reported 'culms (1–)3–10 mm' wide and Van den Berghen (1988: 226, Figure 167A) illustrated a plant comparable with those taken from Lake Nhlabane. Apart from photosynthesis, the function of the filiform culms is unknown.

Tubers

Some races of this species yield edible tubers ('Chinese water chestnuts'). Tubers have not been observed for southern Africa.

Distribution

In southern Africa, *E. dulcis* is known only from Botswana and KwaZulu-Natal. The species is widespread through the tropics of the Old World, China and Japan.

Selected citations

—1923 (Maun): Xhamu lagoon, SW end (–AA), *W Ellery 350* (PRE); Okavango, ± 5 km NE Godikwe lagoon (–AB), *W. Ellery 155* (PRE); Okavango, Boro river N of Maun (–CB), *R.P. Ellis 2734* (PRE); Santantadibe river, 2 ml before junction with Thamalakane river (–CB), *P.A. Smith 201* (PRE); Okavango, Santantadibe river (–CD), *van Rensburg B 4156* (PRE);

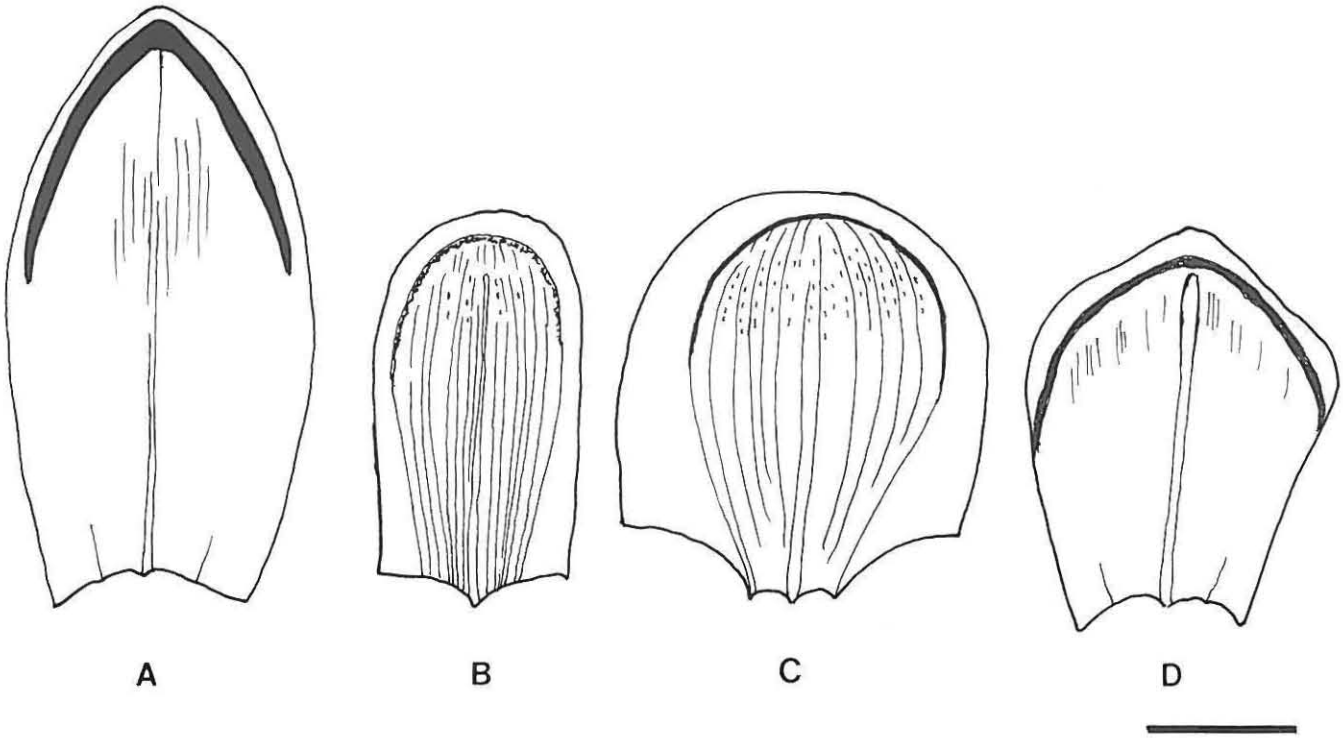

Figure 4 Glumes, flattened, seen from abaxial surface. **A**. *Eleocharis dulcis*. **B, C**. *E. acutangula*. **D**. *E. mutata*. Scale bar. 2mm.

—2632 (Bela Vista); Ingwavuma Distr., Kosi Nature Reserve (–DD), *Tinley 296* (NU).
—2732 (Ubombo): SE of Maputa (–BB), *Strey 8198* (NH, PRE).
—2832 (Mtubatuba): lake Nhlabane, constriction between N & S lakes (–CB), *C. J. Ward & A. Rajh 11459, 11597*; N lake, W shore (–CB), *C.J. Ward & A. Rajh 11464, 11599*; E of N Lake (–CB), *C.J. Ward & A. Rajh 11718* (all NH, NU, PRE, UDW).
—2930 (Pietermaritzburg): Happy Valley Nature Reserve, Wentworth, Durban (–CD), *F. Raiman and C. J. Ward 8* (NU).
—3030 (Port Shepstone): Umdoni Park, natural pond on Golf Course (–CB), *K.D. Gordon-Gray 6240* (NU).
Without precise locality: KwaZulu-Natal, Mhlambanyati Pan, *Michelmore 42* (PRE).

2. ***Eleocharis acutangula*** (*Roxb.*) *Schult.* in Mantissa in volumen secundum systematis vegetabilium Caroli a Linne ex editione J.J. Roemer ... et J.A. Schultes ... curante J. A. Schultes: 91 (1824); Kern: 525 (1974); Haines & Lye: 67 (1983); Vanden Berghen: 221 (1988). Type: from India. *Scirpus acutangulus* Roxb.: 216 (1820), *n.v.*

Scirpus fistulosus Poir.: 749 (1804) non Forssk. (1775). *Eleocharis fistulosa* (Poir.) Schult.: 89 (1824); C.B. Clarke: 198 (1897/98); C.B. Clarke: 406 (1901/02); Svenson: 152 (1929). Type: from Madagascar, non Forssk. (1775), *n.v.*

Perennial, tufted, shoot bases frequently dark red. *Rhizome* vertical, woody, 40–50 × 4–7 mm (old plants) more commonly curved or abbreviated; stolons elongate, up to 400 mm, terminating in an erect shoot, nodose, internodes 20–70 × 3–4 mm, red brown or pallid, nude except for scale leaves up to 10 mm long, soon wearing away; frequently rooting and producing one lateral bud from each node, some of which develop into erect shoots. *Culms* immersed in life except for distal apices, or in shallower marginal situations exposed, erect, frequently twisted, trigonous, flat surfaces faintly longitudinally striate, mid green to glaucous, non-septate, softly firm, compa rtmentalised by tissue strands, not hollow, variable in size, 0.2–1.4 m × 1–7 mm (see also under morphological notes). *Leaves* reduced to prophyll and 1 entire, membranous, dark red to brown, delicate sheath enveloping culm base, prophyll soon fragmenting, upper sheath longer persistent, up to 230 mm (length variable, related to total culm length), mouth oblique, prominently veined below acute apex; ligule lacking. *Inflorescence* a terminal oblong spikelet, cylindric in x-section, up to 45 × 5 mm. *Bract* 1, glumelike, but hard, finely veined, margin membranous. *Glumes* variable, fairly loosely spirally imbricate, sometimes markedly so when glumes wide, broadly oblong to orbicular when detached and flattened, 5.0–5.2 × 2.4–5.0 mm, not keeled, slightly folded basally, coriaceous, grey green becoming pallid, marked abaxially by close-packed, strongly-marked veins, clearly demarcated from dark brown membranous margin that may widen considerably proximally, eventually fading and wearing away, dark dotted adaxially. *Perianth* (perigonium) variable, of 6–3(–2–0) soft, often pinkish bristles united basally into short, soft collar shed with achene, bristles up to ½ achene length, occasionally 1 or more to achene shoulder length, retrorsely spinulose to smooth, OR (especially in more tropical localities) of 6 (–7) yellowish, fine but hard bristles well surpassing achene, sparsely retrorsely spinulose, more often smooth. *Stamens* 3, caducous, anthers 2.7–2.8 mm long with crest 0.3 mm. *Style* flattened, base when fully-formed hat-shaped in profile, but variable in florets of an individual spikelet (see also under morphological notes); branches 3. *Achene* biconvex, vase-shaped in outline (that is obovate, narrowed sub-apically into a short neck about $^1/_3$ of maximum achene width), 1.4–2.0 × 1.2–1.6 mm excluding style-base, glistening stramineous to bright cinnamon brown at maturity, surface ×600 trabeculate, marked by ± 15 longitudinal cell rows on each face, cells wider than deep (Figures 2, 4B, 4C and 7).

Morphological notes, including variability

Stolons

The stolons of *E. acutangula* differ from those of *E. dulcis* in that roots and a shoot bud are produced at many nodes, one or more of the shoot buds often developing into an erect culm comparable with that which terminates the stolon. *E. acutangula* is not limited to the deep water localities required by *E. dulcis*, it usually inhabits more marginal situations in shallower water with more fluctuating levels, but will flourish also where soil is saturated but no visible depth of standing water is present. It may be these

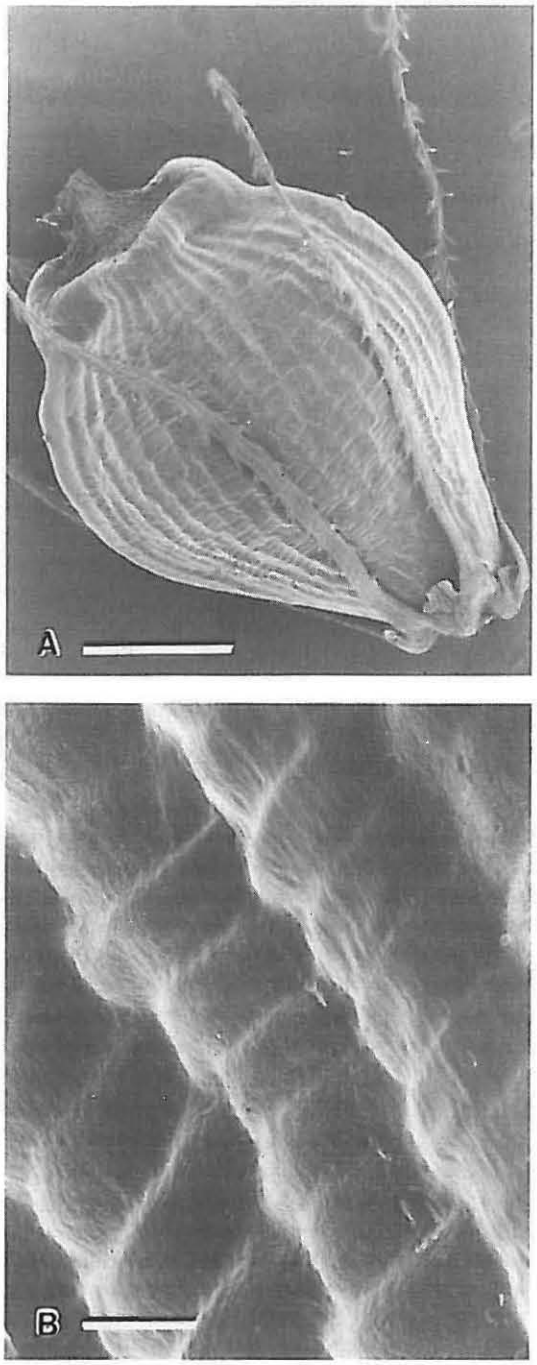

Figure 5 *Eleocharis mutata*. **A.** Achene with perianth and style base. **B.** External topography of pericarp. *C.J. Ward & A. Rajh 1600* (NU). Scale bars A. 500 µm, B. 25 µm.

habitat conditions (of greater light, warmth and oxygen availability) that govern the stolon differences in *E. acutangula* and *E. dulcis*.

Culms

Culm height and width is very variable. Culms in deep water are usually tall and robust (1.2–1.4 m × 5–7 mm); in shallower water usually 0.6–0.7 m × 3–4 mm, but these measurements are no more than a general guide. Culms developed from stolons are always appreciably less robust than those from the parental rhizome. Filiform culms as reported for *E. dulcis*, are not as markedly contrasting in *E. acutangula*, but are quite often present, for example, *Gibbs Russell 1995* (PRE); *W. Jacobsen 4113* (PRE); *S. Mavi 983* (NU ex SRGH) all from Zimbabwe and *Reid 85* (PRE); *Feely & Ward 15* (NU, PRE) from South Africa. Culm angles beneath the inflorescence usually form narrow 'wings'.

Glumes

Glumes, removed and flattened, are variable with gradation between extremes. Differences are in width, shape and colouration, the last being least reliable because of changes taking place with age and drying. Recorded extremes were:

1. 5.0–5.2 × 2.45–2.55 mm, broadly oblong, apex broadly obtuse, slightly projecting, marginal membranous tissue narrow, not widening markedly laterally, usually not very dark brown (Figure 4B).

2. 5.0–5.2 × 4.75–5.0 mm, more or less orbicular, apex rounded, not projecting beyond glume outline, marginal membranous tissue narrow apically, widening markedly laterally, very dark brown and clearly differentiated from central veined green zone (Figure 4C).

Differences are between clones, not within clones. Glume variation did not correlate with perianth bristle length.

Perianth (perigonium)

Within *E. acutangula*, the perianth is variable. Two main extremes of short and long bristles are represented (see descr. pg 4), but according to our observations, there are occasional exceptions falling somewhere within the range, for example, *De Winter & Giess 6979*, *Flanagan 982*, both of which favour the short-bristled type but have bristles to achene shoulder length. We tentatively conclude from the samples we have studied, that the shortbristled form occurs in water bodies where *E. dulcis* is not present; where *E. acutangula* and *E. dulcis* coexist the long-bristled form is frequent, while short-bristled examples are occasional. However, more exhaustive sampling within numbers of isolated water bodies is required to test this preliminary deduction.

Always the perianth of *E. acutangula* differs in texture, in colour and in extent of retrorse barbing from that of *E. dulcis*. The short-bristled perianth is fleshy, soft and yellowish pink, the bristles sparsely barbed or barbless; the long-bristled type is firmer and yellow, the bristles elongate, slender and usually barbless never having the strong hard texture, white colour and pronounced barbing of the perianth in *E. dulcis*.

Style base

The tissue of this organ is predominantly soft and spongy. At maximum development and with the broad face observed in profile, the style base forms a roughly hemispherical hat that covers the neck of the achene (Figure 2A). With drying and ageing there

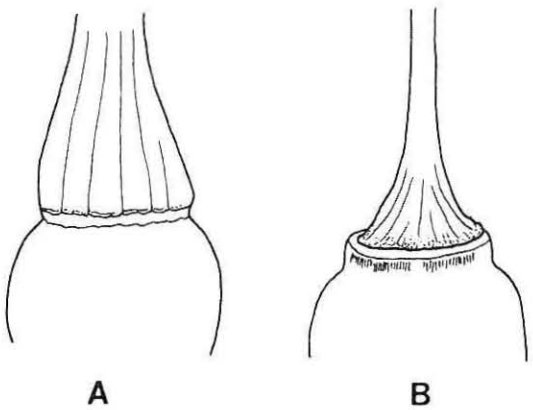

Figure 6 *Eleocharis dulcis*. Variation in style bases. **A**. Turgid before drying. **B**. Shrunken after drying.

is shrinkage and upward curvature so that the basal edge curls up to reveal the achene neck (Figure 7A). In some florets expansion of the style base does not take place (due to non-fertilisation of the ovule?); it is then triangular (in profile) and shrunken within the rim of the achene neck. These variations frequently occur within an individual spikelet.

Achenes

The achenes are narrowed distally into a short neck about one-third of maximum achene width. This neck may be concealed by a fully developed, turgid style base. The achene surface always shows trabeculate patterning, but cells vary in their length/width relationship and also the number of longitudinal rows per achene face (both these criteria are difficult to express statistically because of problems of accuracy in evaluation). At full maturity, the achenes become a shining dark brown, with the exocarp cells somewhat inflated.

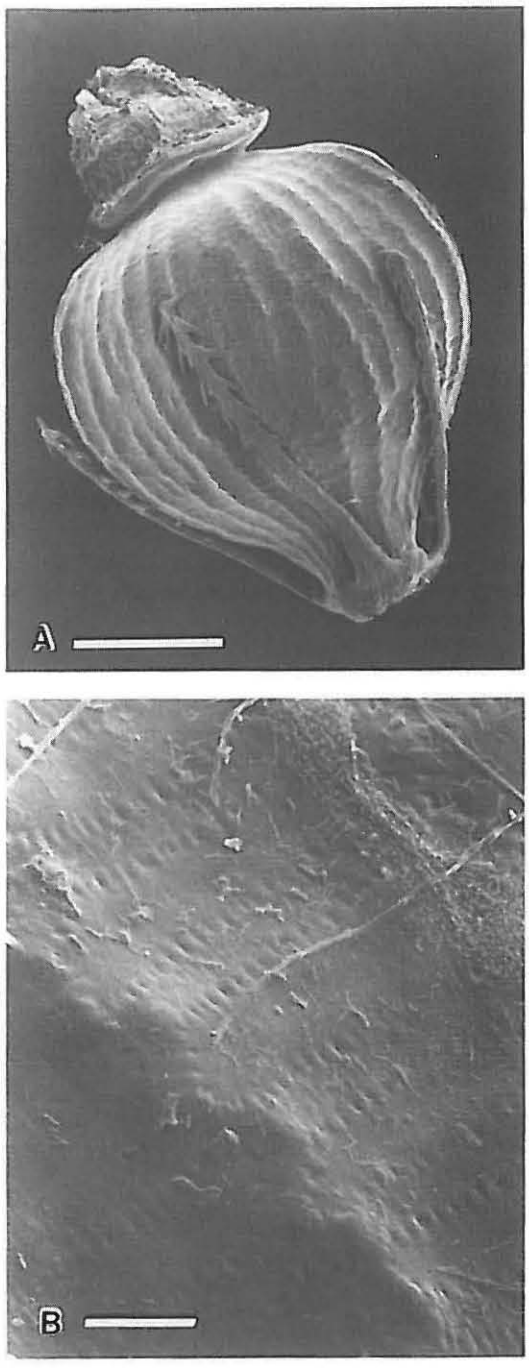

Figure 7 *Eleocharis acutangula*. **A**. Achene with pericarp and style base. **B**. External topography of pericarp. *C.J. Ward 11926* (NU). Scale bars. A. 500 µm, B. 25 µm.

Distribution

In southern Africa, *E. acutangula* is widely distributed being absent only from the Free State where plants may have been overlooked, and Lesotho, where climatic conditions may be too cold.

Selected citations

Form with perianth bristles about half achene length or less

—**1816** (Namutoni): shallow pan near Oneina Mission Station, 18 ml SE Ondangua (–AA), *De Winter & Geiss 6979* (PRE) (occasional bristle attaining achene 'shoulder' length).
—**1922** (Nokaneng); Okavango delta, Karonga River (–CB), *P.A. Smith 1418* (PRE).
—**2321** (Lehututu): Botswana, Mahu (Mahung ?) Pan (–DA), *P.A. Smith 498* (PRE).
—**2330** (Tzaneen): Kruger National Park, Mahlambandlopfu Pan (–BD), *van der Schijf 2861* (PRE).
—**2428** (Nylstroom): Waterberg, 13.2 m NW Warmbaths, *Acocks 23562* (PRE); Naboomspruit, Mosdene Farm (–DB), *Germishuizen 46* (PRE).
—**2632** (Bela Vista): Ingwavuma distr., Ndumu Game Reserve, near Balumhlanga (–CD), *Pooley 1624* (NU).
—**2732** (Ubombo): Tembe Elephant Park, Kwa Msomi (–AB), *M. C. Ward 2762* (NH); Maputaland, Sileza Forest Reserve, eastern boundary (–BA), *Matthews 1188* (NU, PRU).
—**2832** (Mtubatuba): Hlabisa distr., St Lucia, eastern shores (–BA), *Feely & Ward 15* (NU,PRE).
—**2930** (Pietermaritzburg): Greytown, Merthley Lake (–BA), *Musil 547* (PRE); Howick area, Gartmore Farm (–AC), *P.B. Taylor 131* (NU); Durban area, Umlaas Settlement Ponds (–DC), *C. J. Ward 11925, 11926* (NU, UDW).
—**3228** (Butterworth): Kei Mouth (–CB), *Flanagan 982* (PRE) bristles to 'shoulders' of achene.

Form with perianth bristles surpassing achene length

—**1923** (Maun): Botswana, Okavango, 5 km NE of Godikwe lagoon (–AB), *W. Ellery 153* (PRE); Okavango, Txatxanika lagoon (–AB), *Gibbs Russell & Biegel 1484* (PRE).
—**2530** (Lydenburg): Nelspruit distr., Witkop Staatsbos, Witklip Dam (–BD), *Kluge 862* (PRE).
—**2631** (Mbabane): Malototja Nature Reserve, below Mortimer's Dam stream (–AA), *Heath 406* (PRE).

3. ***Eleocharis mutata*** (L.) *Roem. & Schult.*, Systema vegetabilium (Caroli a Linné) 2 (1817): 155; Svenson: 133 (1929); Hooper: 314 (1972); Haines & Lye: 66 (1983). Type: Jamaica, *Elmgren* (LINN, photostat !).

Scirpus mutatus L.: 391 (1759); L.: 71 (1762). *Limnochloa mutata* (L.) Nees: 294 (1835).
Eleocharis fistulosa sensu C.B. Clarke: 406 (1901/02) partly, non (Poir.) Schult.

Perennial, tufted, with the vegetative characters of *E. acutangula* including stolons with roots and lateral buds at nodes. *Inflorescence* an oblong, cylindric spikelet, tapering slightly distally, 22–40 × 3–4 mm. *Bract* 1, hard, without obvious venation, 4–6 mm deep, edges folding over and enveloping spikelet base as collar. *Glumes* closely spirally imbricate, appearing wider than long (much of length hidden by overlap), when detached and flattened obovate to almost square (depending upon width of truncate base), 4.0–4.8 × (2.5–)3.0–3.5(–4.5) mm, apex broadly obtuse with central area slightly peaked, firm to hard, lacking obvious veins except for central midvein forming

slightly projecting keel terminating below membranous apical edge (clearly visible adaxially), grey green, with dark brown to black submarginal line below membranous pallid edge, becoming uniform yellowish to pallid brown in age, lacking gland dots. *Perianth bristles* usually 6, often with softer retrorse barbs, otherwise as for *E. dulcis*. *Stamens* 3; anthers 1.65–2.25 mm, crest 0.3 mm. *Style base* almost long pyramidal as for *E. dulcis*, but smaller and fitting into upturned infolded rim of achene; style branches 3. *Achene* obovate, occasionally more urn-shaped (as for *E. dulcis*), biconvex, constricted subapically into clearly-defined thick rim just wider than ½ achene width, 1.9–2.2 × 1.4–1.6 mm excluding style base; dark brown, not glistening; surface finely trabeculate, marked by numerous, closely placed longitudinal ridges linked by faint cross lines, cells slightly wider than deep, some almost isodiametric (Figures 3, 4D and 5).

Morphological notes

In its perennial stoloniferous growth form and sharply trigonous culms, *E. mutata* is indistinguishable from *E. acutangula*. Its floral features differ, however, in that there is resemblance to *E. dulcis* in the perianth, achene and style base (see Table 1 and contrast Figures 1, 5 and 7). It is interpreted as of hybrid origin, representing approximate intermediacy between its putative parents, *E. dulcis* and *E. acutangula*. As a species it is of long stand-

Table 1 *Eleocharis mutata*: main morphological characters in comparison with those of *E. dulcis* and *E. acutangula* (all measurements in mm). (Note that the variation in perianth for *E. acutangula* is omitted for convenience)

Character	*E. dulcis*	*E. mutata*	*E. acutangula*
stoloniferous perennial	yes	yes	yes
Culm			
septate	yes	no	no
hollow	yes	no	no
shape in cross section	terete	sharply trigonous	sharply trigonous
Glume			
size (extremes) l × b	7.0–8.0 × 4.0–4.5	4.0–4.8 × (2.5–)3.0–3.5 (–4.5)	5.0–5.2 × 2.4–5.0
shape in outline when detached and flattened	narrowly oblong–elliptic	obovate to almost square	broadly oblong–orbicular
venation	not keeled; veins faint, fine	slight keel that terminates below membranous margin	not keeled; veins close packed, strongly marked
membranous margin and flanks	membrane margin narrow; flanks little widened	membrane margin narrow; slightly peaked above keel; flanks usually widened basally	membrane margin narrow; flank width variable; often markedly widened basally
dark dotting	lacking	lacking	present
Perianth			
collar	well developed, firm	well developed, firm	poorly developed, soft
number bristles	7	6	6–3(–2–0)
bristle length	surpassing achene	surpassing achene	typically up to half achene length, occasionaly 1–2 reaching achene shoulder length
retrorse barbs	many, strongly developed	many, barbs softer than for *E. dulcis*	sparsely barbed or smooth
Style base			
outline shape	long pyramidal	long pyramidal, but smaller than for *E. dulcis*	hat-shaped
variation on drying	shrinking, narrowing	shrinking into achene rim	edge curling up to reveal achene neck
style branch number	3	3	3
Achene			
outline shape	urn-shaped to elliptic	usually obovate, less often urn-shaped	obovate, narrowed subapically into neck about one third achene width
apical rim width	just wider than half achene width	just wider than half achene width	just wider than neck
surface topography	smooth	finely trabeculate	trabeculate
colour	pale brown–brown	pale brown–brown	shining cinnamon brown

ing but it is nowhere common or extensive. The conformation of the glumes, achene apex and style base have been relied upon in distinction from *E. acutangula*, (Hooper 1972: 312; Haines & Lye 1983: 65), but these characters are difficult to assess because of the range of variability encountered. The trigonous, non septate culms set it apart from *E. dulcis*.

E. mutata differs from *E. variegata* in its glumes, achene apex, style base and achene surface texture. There are also differences in the perianth, but the long-bristled expression of this in *E. variegata* differs only in degree of robustness and colour from that in *E. mutata*.

It is probable that examples with the floral characteristics of *E. mutata* have been included within *E. acutangula* when the culms are sharply trigonous and non septate; within *E. variegata* when the culms are terete and non septate, and within *E. dulcis* when culms are terete and septate.

Distribution

In southern Africa, *E. mutata* has been reported only from KwaZulu-Natal. Probably it is also present in Botswana, in the Okavango swamps where *E. dulcis* and *E. acutangula* co-exist and where numerous long-bristled variants of *E. acutangula* are already known. It is present in Tanzania and on adjacent off-shore islands, in West Africa and Zaire. There are records also from the West Indies, Central America and northern South America, in fact wherever there is likely to be co-existence of *E. dulcis* and *E. acutangula*.

Selected citations

—2832 (Mtubatuba): Lake Nhlabane, S of St Lucia estuary (–CB), *C.J. Ward & A. Rajh 11600*; *C.J. Ward & G.W. Begg 11715, 11717* (K, NH, NU, PRE, UDW).

4. ***Eleocharis variegata*** (Poir.) *Presl* in Isis, oder Encyclopädische Zeitung von L. Oken ed. 21: 269 (1828); Kunth: 153 (1837); Svenson: 156 (1929); Brain: 84 (1934); Svenson: 8 (1939); J. & A. Raynal: 319 (1967); Hooper: 314 (1972); Kern: 528 (1974); Haines & Lye: 68 (1983). Type: Madagascar, Petit-Thouars (P), *n.v.*

Scirpus variegatus Poir.: 749 (1804).

Perennial, tufted, shoot bases brown or suffused dark red. *Rhizome* and stolons as for *E. acutangula*, but less robust and shorter in all their parts. *Culms* immersed in life except for distal apices, or mostly exposed, erect, generally terete, sometimes subtrigonous or subquadrangular grading to subtriangular below inflorescence, occasionally twisted, non septate, spongy, compartmentalised internally, up to 0.5 m × 3(–4) mm. *Leaves* reduced to prophyll and 1–2 entire, membranous delicate sheaths enveloping up to lowest $^1/_3$ culm length; mouth oblique to cuneate; ligule lacking. *Inflorescence* up to 24 × 4 mm. *Glumes*, loosely spirally imbricate at maturity of achenes, broadly oblong when detached and flattened, 4.5–5.0 × 3.0 mm, not keeled, slightly folded basally, central proximal zone coriaceous, glaucous green to pallid, frequently suffused deep purplish-red, closely longitudinally veined (more faintly than in *E. acutangula*), distal zone a deep (up to 1 mm) membranous flap with margin broadly obtuse, rounded, sometimes erose, continuing into lateral flanks that may be deep purplish-red or pallid, liberally dotted with small dark dots (glands or resiniferous cells?), the membranous zone easily fragmenting, eventually wearing away. *Perianth* variable, commonly a poorly developed, pinkish collar with 1–7 minute outgrowths (reduced bristles) or the collar entirely lacking (occasionally 1–3 bristles develop to ½ achene length), sparsely barbed; OR a slender collar bearing 7–8 fine, retrorsely-barbed whitish-yellow bristles that are twice as long as the achene. *Stamens* 3, filaments at anthesis surpassing achene, often persistent; anthers 1.5–2.8 mm long, minutely crested. *Style* base persistent, ± triangular in profile, cells usually

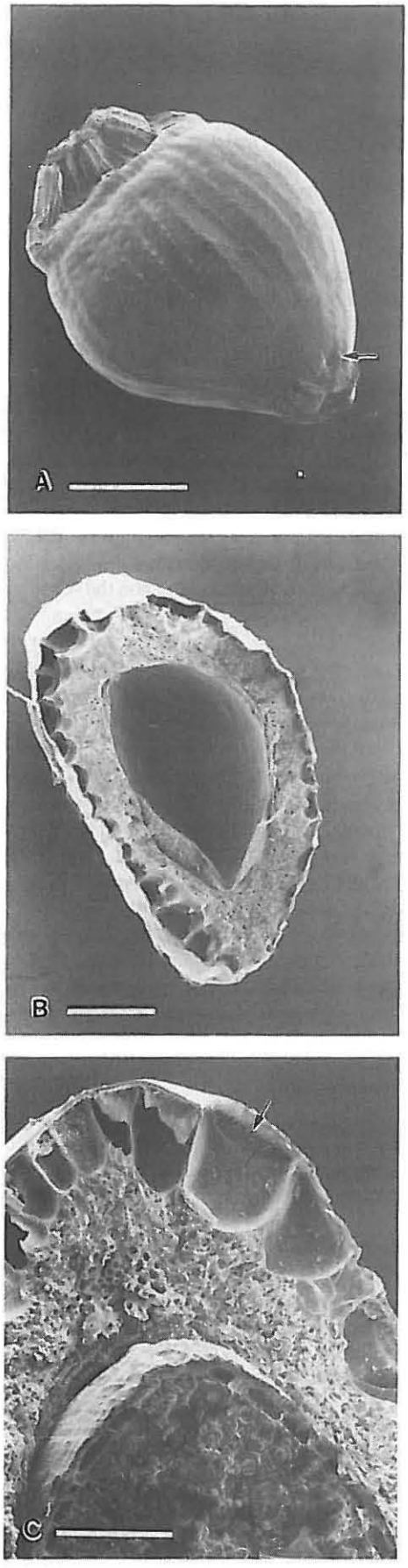

Figure 8 *Eleocharis variegata*. **A**. Achene with perianth (one bristle arrowed) and style base. **B**. Achene in transverse section. **C**. Portion of achene and seed in transverse section (enlarged exocarp cell arrowed). A, C. *C.J. Ward 11716* (NU). *B. Smook 6138* (PRE). Scale bars. A. 500 µm, B. 250 µm, C. 100 µm.

shrunken, dark coloured, fitting distal rim of achene; style branches 3 or 2 in same inflorescence. *Achene* biconvex to faintly subtrigonous, elliptic in profile with distal rim ± total achene width, glossy, pale to dark cinnamon brown; surface almost smooth to longitudinally striate; exocarp cells translucent (except when cinnamon brown), inflated (Figures 8 and 9A).

Morphological notes, including variability

E. variegata bears relationship to *E. acutangula* in its general morphological facies, but plants are mostly smaller and less robust, and with culms frequently not triangular. Stolons root and shoot from the nodes.

Culms

Culms are most commonly terete, but they lack the externally defined transverse septa of *E. dulcis* and are not hollow, possessing the compartmentalised anatomy of *E. acutangula*. Frequently there is variation from terete to subquadrangular to subtrigonous, the angles being rounded and poorly defined, or sharper, especially immediately beneath the infiorescence, but seldom is there projection of these angles as short wings as in *E. acutangula*. Often there is some degree of spiral twisting. As water levels fall culms may lodge, somewhat coiled, upon the substrate.

Leaves

Haines & Lye (1983: 68) state 'sheaths about 3 above the prophyll.' We have not clearly observed three sheaths in our study, but these are allowed for in the formal description.

Glumes

Glumes are characteristic of the species. When detached and flattened, the broadly oblong shape and well developed distal membranous edge up to about one-third of total length, and the liberally scattered dark dots (glandular or resiniferous?) are distinctive. So, too, is the colouration when fully expressed, namely, a central glaucous veinless area flushed reddish purple, the flushing continuing distally and laterally into the membranous zone. But these pigments are not always evident and also fade with age and herbarium storage. The glumes of *E. acutangula* have a far narrower membranous distal margin.

Perianth (perigonium)

The perianth, as in *E. acutangula*, is variable. Commonly, it is a rudimentary expression of the short-bristled form of *E. acutangula* being an inconspicuous pinkish or cream collar, with up to 7–8 very short projections surrounding the fruit base (Figure 8A arrow) OR the collar may be entirely lacking. Other examples, particularly from the Okavango, exhibit bristles surpassing the achene by almost another achene length, whitish-yellow, strong and clearly retrorsely barbed. These two expressions reflect the comparable variation within the perianth of *E. acutangula*.

Style base and style branches

The style base forms a junction with the wide mouth of the achene, which is never narrowed into a neck as in *E. acutangula* and *E. decoriglumis*; it meets the upstanding achene rim, eventually shrinking into it and does not overlie the achene tissue at all. Style branch number is variable (2 or 3), even within a single spikelet, the branches being long and amply provided with elongate papillae.

Achenes

The achenes differ in outline shape from those of *E. acutangula* when viewed from the broad face. Each has a wide distal mouth only marginally narrower than maximum achene width. In this feature there is relationship with *E. mutata* and *E. dulcis*. Surface conformation is ill defined; a series of faint longitudinal ridges with the transverse walls of the cells between the ridges barely marked. The trabeculate patterning of *E. acutangula* is therefore present, but muted, as can be observed in Figure 8A in which the almost flat outer periclinal surface to the exocarp is evident. The exocarp cells are radially quite deep (Figure 8C arrow) which contributes to the somewhat inflated and translucent appearance of the achene before it has darkened to a shining brown, similar in colour and gloss to fully mature achenes of *E. acutangula*. Between the initial glossy cream of an unripe achene and the glowing brown of one fully mature, stages are visible in which the cell walls darken, to clearly define the trabecular patterning against a lighter background.

Distribution

In southern Africa, *E. variegata* occurs most commonly in the Okavango area of Botswana. There are isolated records from the Transvaal, KwaZulu-Natal and the E. Cape. Extraterritorially, the species is known from tropical East and West Africa, Madagascar, Mauritius and the Seychelles. Hooper (1972: 314) reports 'Intermittently throughout the tropics.' Kern (1974: 528) finds it 'only a few times collected' in Malaysia.

Selected citations

Form with short bristles or lacking a perianth

—**1923** (Maun): Botswana, Okavango, Didinga island (–AA), *W. Ellery 297* (PRE); Okavango, flood plain of Mboroga R. (–AA), *P.A. Smith 2914* (PRE); Mboroga flood plain, *Biggs M721* (PRE); Okavango, last 2 ml of Santantadibe R. before joining Thamalakane R. (–DC), *P.A. Smith 217* (PRE).
—**2428** (Nylstroom): Moord drift, in dried up vlei of Nyl R. (–BD), *Mauve 4283* (PRE).
—**2929** (Underberg): Champagne Castle (–AB), *Strey 7824* (PRE).
—**3129** (Port St Johns): Mkambate Nature Reserve (–BD), *Smook 6138* (PRE).

Form with bristles surpassing achene length

—**1822** (Kangara): Botswana, Gum Ledeba (–CD), P.A. Smith 1569 (PRE).
—**1923** (Maun): Okavango, bog N. of Godikwe island (–AA), *W.*

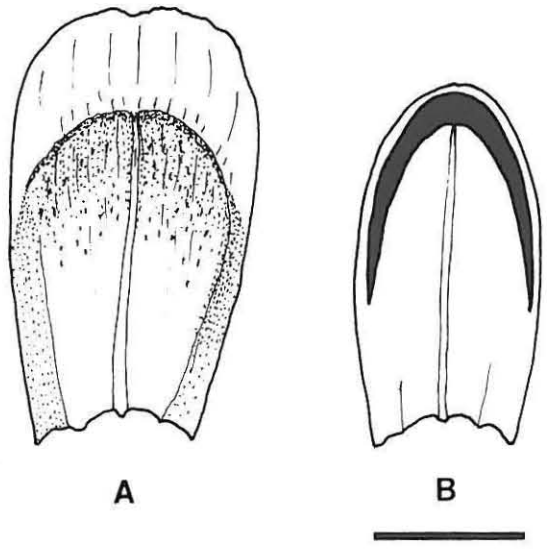

Figure 9 Glumes, flattened, seen from abaxial surface. **A.** *Eleocharis variegata*. **B.** *E. decoriglumis*. Scale bar 2 mm.

Ellery 342 (PRE); Okavango, edge of Xobega R. (–AA), *P.A. Smith 2813* (PRE); 500 m upstream Xobega lagoon (–AA), *W. Ellery 174A* (PRE); Xobega lagoon (–AB), *Gibbs Russell 1506* (PRE); Okavango, s. outflow Txatxanika lagoon (–AB), *W. Ellery 28* (PRE).

Examples of citations that indicate the sympatry of:

1. *E. dulcis*, *E. acutangula* and *E. variegata*

—**1923** (Maun): Okavango, ±5 km NE Godikwe Lagoon (–AA), *W. Ellery 153* [*E. acutangula*]; *154* [*E. variegata*]; *155* [*E. dulcis*] (all PRE); Santantadibe R before joining Thamalakane R (–CD), *P.A. Smith 201* [*E. dulcis*]; (–DC), *202* [*E. acutangula*]; (–DC), *217* [*E. variegata*]; along Santantadibe R. (–CD), *van Rensburg 4155* [*E. acutangula*]; *4156* [*E. dulcis*].

2. *E. dulcis, E. mutata, E. variegata* and *E. acutangula*

—**2832** (Mtubatuba): Lake Nhlabane, S of St Lucia Estuary (–CB), *C. J. Ward & G. W. Begg 11715, 11717* [*E. mutata*]; *11716* [*E. variegata*]; *11718* [*E. dulcis*] all from deep water. From shallow water at lake margin *C.J. Ward & G. W. Begg 11378* [*E. acutangula*]. (K,NH, NU, PRE, UDW).

5. ***Eleocharis decoriglumis*** *Berhaut* in Bulletin de la Société Botanique de France 100: 174 (1953); Berhaut: 363 (1967); Hooper; 314 (1972); Haines & Lye: 70 (1983); Vanden Berghen: 223 (1988). Type: Senegal, without precise locality, *Perrotet 839* (P., Herb. E .Drake, isotype)!

Annual tufted, shoot bases sometimes reddish. *Rhizome* abbreviated, connecting shoots, bearing numerous, rather fine adventitious roots. *Culms* erect, indistinctly 3-angled (ridges pronounced below inflorescence) non-septate (spongy internally) up to 450 × 2–3 mm, noticeably variable in height within a tuft, olive green, glabrous. *Leaves* reduced to prophyll and 1 entire, membranous, delicate sheath enveloping each culm base; mouth truncate to oblique terminating in a minute projection; ligule lacking. *Inflorescence* a terminal oblong to linear spikelet, scarcely wider than culm, cylindric in x-section, up to 30 × 3 mm. *Bract* 1, glume-like but slightly larger, fertile (in examples studied). *Glumes* fairly loosely spirally imbricate, 4.2–4.8 × 2.0–2.3 mm, oblong-elliptic, slightly concave with poorly marked rounded keel, midrib indistinct externally, visible internally, faintly striate with numerous close veins, olive green with distinctive dark brown almost black margin up to 0.5 mm deep, apex rounded. *Perianth* 7–9 strong bristles, 2 ranked, expanded basally to form a 'collar' shed with achene, bristle length equalling or slightly shorter than achene without style base, strongly retrorsely spinulose. *Stamens* 2, not always maturing together, anthers 0.7–0.8 mm long. *Style* flattened, base hat-shaped, about 0.7 × 1.3 mm, persistent on achene, dark brown, branches 2. *Achene* biconvex, broadly obovate (vase-shaped) in outline, constricted apically into a very short neck carrying persistent style-base (as style base dries and lifts the constriction becomes visible) 1.5–1.6 × 1.2–1.3 mm excluding style base, lustrous cream when young, developing brown markings, eventually dark shining brown; surface marked by 18 or more longitudinal rows of isodiametric ±6-sided cells (Figures 9B and 10).

Morphological notes

In southern Africa *E. decoriglumis* is inadequately known. It is described as annual, tufted, with a slender root system. It certainly appears to lack the stolons of all other species of Section *Limnochloa* treated in this article. It also favours shallow water habitats with impermanent levels and therefore is probably seasonal. Further investigation is desirable to determine the duration of survival of the tufts and whether any subterranean tissue endures to regenerate under the stimulus of favourable conditions.

There is relationship with *E. variegata*, and less directly *E.*

Figure 10 *Eleocharis decoriglumis*. **A**. Achene with perianth and style base. **B**. Surface topography of pericarp. **C**. Portion of pericarp in transverse section. *P.A. Smith 1900* (NU). Scale bars. A. 500 μm, B. 25 μm, C. 100 μm.

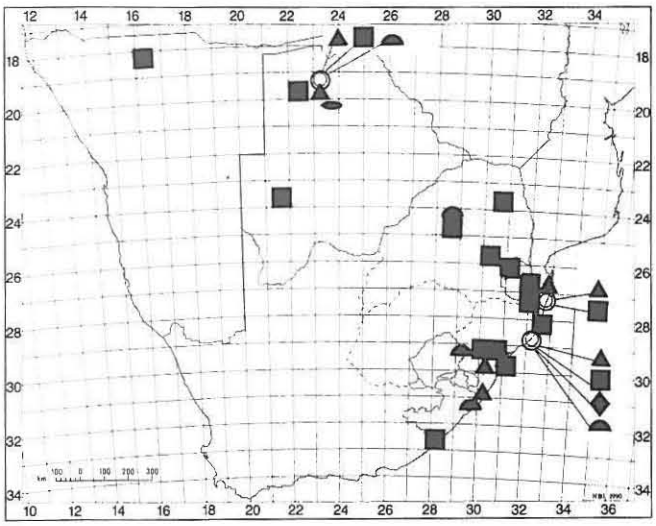

Figure 11 *Eleocharis* subgen. *Limnochloa* sect. *Limnochloa*. Known distributions of species in southern Africa.
Key: ▲*E. dulcis* ■ *E. acutangula* ◆*E.mutata* ◠*E.variegata* ▬ *E. decoriglumis* ◎Sympatry of species

acutangula, in the indistinctly trigonous culms which become more markedly angled beneath the inflorescence. Florally, relationship is with *E. acutangula*, particularly in the achene shape with its narrowed base and clearly defined distal neck over which extends the wider, hat-like style base. The strongly developed, white, retrorsely scabrid perianth bristles relate most closely, in the robustness of the collar, to *E. dulcis*. In the number of stamens and style branches *E. decoriglumis* is individual within section *Limnochloa*. Haines & Lye (1983: 70) describe a solitary stamen per floret. Our study has revealed two, but these at different stages of development. Style branches are consistently two.

The most readily observed feature, the dark, purple-brown to black band to the glume gives a beautiful patterning to the young spikelet that makes the species worthy of cultivation. It is not considered reliable in its own right as a solitary feature of identification, however, as in other species of the section colour is usually variable, and certainly fades with age and with preservation in herbaria.

Distribution

In southern Africa, *E. decoriglumis* is known only from Botswana, from where it was recently reported (Browning *et al.*, 1995: 238). Specimens collected in 1977 from drying, clay-floored pans in the Boteti River floodplain had been tentatively placed with *E. variegata* and *E. acutangula*. An African endemic, *E. decoriglumis* is also known from West and East Tropical areas of the continent; it is always rare and localised.

Selected citations

—**2023** (Kwebe Hills); Boteti R, below Samadupe bridge (–BA), *P.A. Smith 1900* (NU, PRE, SRGH); *Ellis 2980* (PRE).

A map of known distributions in southern Africa of the five species dealt with in this article is given (Figure 11).

Discussion and Summary

Of the five species included within *Eleocharis* subgen. *Limnochloa* section *Limnochloa* in southern Africa, *E. dulcis* is probably the most distinctive on account of its robust, terete, airfilled culms marked by transverse septa that become closer together towards the culm apices. The acutely trigonous, soft spongy but non-septate culms of *E. acutangula* are also distinctive and in strong contrast. However, use in isolation of these so easily observed 'markers' is often misleading as it leads to non study of the variable floral morphology that exists. Especially is this applicable to *E. acutangula*, which in southern Africa and as presently delineated elsewhere, is extremely variable. Detailed examination of florets and of mature achenes is required to reveal the similarities and differences among the five taxa as they are recognized in this article. Then, it becomes apparent that species limits are not clearly defined. *E dulcis* is readily identified by its culm structure, but florally there is some variation in achene shape, achene apex and style base conformation. This is a deep water species that is not easily sampled: it is limited to the more tropical areas of southern Africa (Botswana and KwaZulu-Natal) and it is possible the limits of its variation in these locales have not yet been fully revealed. That *E. dulcis* is variable, is clearly apparent from the literature where statements as 'It is possible several entities are involved in this widely distributed species' (Svenson, 1929: 159), and 'Undoubtedly several races are involved in this widely distributed ... extremely polymorphic species' (Kern 1974: 531), are frequent.

The features used almost exclusively in existing classifications and keys to identification of the taxa within section *Limnochloa*, apart from culm construction, namely the conformation of the achene apex and persistent style base, fall into two groups; one with wide-mouthed achene to which the style base is attached and into which it shrinks (*E. dulcis*; *E. mutata*; *E. variegata*); the other with achene narrowed into a neck less than half achene width, over which the style base extends (*E. acutangula*; *E. decoriglumis*). However, the differences are not as pronounced as words suggest and careful observation of several examples from different spikelets is recommended if accurate decisions are to be made, especially as changes in style base conformation take place with maturation of the fruit, or not, and with drying and preservation of exsiccatae in herbaria. The achene mouth of *E. mutata* is similar to that of *E. dulcis* (see Figures 5A and 1A); the mouth of *E. variegata* is almost achene width (Figure 8A). Observation at magnifications of × 30–40 is needed. Surface topography of mature achenes is also useful in species differentiation. Again *E. dulcis* is the most distinctive with surface contouring smooth or faintly revealing the longitudinally quadrangular shape of the underlying exocarp cells. All other species exhibit variation of the trabeculate surface as it is represented by the achene of *E. acutangula*. *E. decoriglumis* has square exocarp cells; others have cells transversely oblong, but in *E. mutata* the cells are very small, the longitudinal rows numerous and usually clearly defined but difficult to count. Achene colouration is not entirely reliable as there are changes according to degree of maturation.

The perianth (perigonium) is difficult to assess in species delimitation. Svenson (1929:126) stated 'the degree of variation [of bristles] is a character confined to the individual species'. He also maintained their texture within a species was constant, 'and this texture may prove to be one of the most valuable means of identification'. (Svenson 1929:126). *E. acutangula* and *E. variegata* both incorporate considerable variability in the perianth, but the soft texture and pinkish brown colouration of the bristles in the short-bristled form within *E. acutangula* (see description pgs 4 and 8), is present in the short-bristled form within *E. variegata*. This texture and the poor development of retrorse barbs is again evident in the long-bristled form within *E. acutangula*, but in the long-bristled form within *E. variegata*, the bristles are firmer, whitish-yellow and well provided with retrorse barbs—suggestive of the bristles encountered in southern African examples of *E. dulcis*. Glume conformation is also useful in species delimitation, but requires careful observation as in some taxa, for example, *E. acutangula*, there is variability. Glume colour may be very

distinctive but is not entirely reliable, as there is always a range in development and a degree of fading with natural ageing and artificial preservation.

Discussion of variability

Where *E. dulcis* and *E. acutangula* co-exist within a water body, or a series of interconnected water bodies, as in the Okavango swamps or Lake Nhlabane, variants are also present: some of these conform within the limits of described taxa; others add to the range in variability encompassed within described taxa; others suggest the need for the establishment of additional taxa. The variation already documented for entities worldwide that must be placed within section *Limnochloa* is extensive and is difficult to accommodate within strict taxonomic classification. Its cause, or causes, so far lack adequate explanation. They need investigation and comprehension.

Our studies have led us to speculate that the main cause of this variation lies in natural hybridisation. We tentatively conclude that within *Eleocharis* isolating mechanisms that prevent natural gene exchange are poorly developed, so that within a water body, or a series of closely associated bodies, hybridisation between species is probable. With the capacity for vegetative multiplication that most species of the genus possess, and the range in microhabitat that most water bodies provide, hybrid progeny are capable of survival together with parental taxa. Over many seasons and with climatic fluctuations, introgression is likely to have resulted in a particular set of variants for a particular water body, the actual constituents dependent upon many interacting factors peculiar to that particular habitat. In support of these contentions we cite the evidence of hybridisation in the wild between species that would normally be regarded as too distantly related to permit the effective survival of progeny (Catling 1994: 837); the presence of polyploidy within the genus (Tucker 1987: 388) and the presence within some species, at least, of polycentric chromosomes, the adaptive value of which in aneuploid (agmatoploid) change is by no means understood (Grant 1971: 264, 270). There is also the repeated evidence of sympatry within a waterbody of *E. dulcis*, *E. acutangula* and *E. variegata* provided without awareness, it would seem, by collectors (see citations under *E. variegata* pg. 9).

We maintain five species within section *Limnochloa* for southern Africa, all already established and represented extra-territorially. *E. dulcis* and *E. acutangula* appear to be the putative parents of *E. mutata*, a taxon only recently recorded for southern Africa (Browning et al. 1995: 238) and which we believe, on the basis of morphology, to be of hybrid origin (Table 1). We note that this species antedates its putative parents nomenclaturally; it has also been selected the lectotype of subgenus *Limnochloa*. *E. variegata* we also speculate as of hybrid origin with *E. acutangula* one putative parent, the other at present unknown, but possibly *E. dregeana* Steud. which appears to be present with *E. acutangula* in habitats where *E. dulcis* has not been recorded, for example, Greytown, Merthley lake; Howick, Gartmore Farm; Underberg, Champagne Castle. Too little is known of *E. decoriglumis* (also newly reported for southern Africa, Browning *et al.* 1995: 238) at present to postulate its origins, except extremely tentatively. It also gives evidence in its morphology, especially its achene and style base conformation, of derivation from *E. acutangula*. *E. acutangula* itself is extremely variable and incorporates at least one form (the long, smooth-bristled form frequently recorded from the Okavango swamps) that may foreshadow an emerging taxon that with time, may require taxonomic recognition.

There are other variants that are not easily placed in already established taxa because of a non-conforming assortment of morphological characters. Where, for example, should stoloniferous perennials with terete, non septate culms and the floral characters of *E. mutata* be placed? Apart from *E. dulcis*, which in southern Africa at least, is reasonably clearly defined, (but this might be an over simplification of what does exist in nature), the other species recognised here represent little more than aggregations of a particular form within a sparser welter of other variants; in other words species limits are not represented by clear discontinuities in morphological assortments. In conclusion we stress the need to obtain more complete understanding of the causes of variation within *Eleocharis* section *Limnochloa* before further variants are given formal taxonomic status. Already, in each continent where elements of section *Limnochloa* are present, nomenclatural proliferation has taken place in attempts to accommodate the main morphological expressions observed.

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